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Citation	PUBLICATIONS OF THE SETO MARINE BIOLOGICAL LABORATORY (1973), 20: 111-132
Issue Date	1973-12-19
URL	http://hdl.handle.net/2433/175785
Right	
Type	Departmental Bulletin Paper
Textversion	publisher

REDISCOVERY OF AN ENIGMATIC OCTOCORAL, *PSEUDOGORGIA GODEFFROYI* KÖLLIKER, FROM SOUTHERN AUSTRALIA AND A DISCUSSION ON ITS SYSTEMATIC POSITION[1]

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With 6 Text-figures and 1 Table

Abstract

Specimens of an octocoral of blade-like form, recently collected by Mrs. Jeanette E. WATSON of the National Museum of Victoria from eastern south coasts of Australia, have been examined and revealed to be *Pseudogorgia godeffroyi* KÖLLIKER, that was once reported in 1870 from St. Vincent Gulf in South Australia, but has never been recorded again for nearly a century and has been forgotten and neglected in recent treatments of the Octocorallia. Concerning its systematic position, KÖLLIKER himself considered to be intermediate between Gorgonacea, Alcyonacea and Pennatulacea, but did not suggest a family affiliation. A few later authors treated this genus have attributed it to the *Telesto*-allies, though it is suspectable that they referred wholly to KÖLLIKER's original description.

The outstanding characteristics that a colony has a single axial polyp which alone has the gastric cavity extending to the base of the colony as a distinct axial canal, short lateral polyps imbedded in the spiculiferous coenenchyme, no axis and no creeping stolon decline to ascribe *Pseudogorgia godeffroyi* to any Octocorallian taxa currently diagnosed.

The present octocoral is regarded to deserve criteria of a special order within the Octocorallia, apart from the Telestacea, and for this we propose to establish a family Pseudogorgiidae and further a new order Gastraxonacea as an intermediate form between Telestacea and Gorgonacea.

Introduction

Recently Mrs. Jeanette E. WATSON, the honorary associate and hydroid specialist at the National Museum of Victoria, Melbourne, Australia, obtained a number of blade-like unbranched octocoral during her scuba diving survey near the Dorothea Island in the Investigator Strait, South Australia, in January 1969. She entrusted them to Dr. Motoki EGUCHI for identification by a specialist, when he visited to Melbourne in January 1970. After returning home, he kindly offered to the senior

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author (H.U.) all of the specimens, 7 in all, for identification and detailed examination. In the next year (January 24, 1971), Mrs. Watson further obtained three fresh specimens of the same octocoral at the Investigator Strait (Diving Survey Station 415), and then forwarded them to the senior author, together with three old specimens, apparently of the same octocoral, which had been obtained off Lakes Entrance, faced to the Bass Strait, Victoria, and now deposited in the National Museum of Victoria.

All these specimens, apparently of the same species, have peculiar characteristics which decline to ascribe them to any octocorallian taxa currently diagnosed. The junior author (E.H.) made the detailed investigation on the internal structure of the colony on microtome sections. On examination in cooperation with the senior author's taxonomical survey, it was revealed that this aberrant octocoral here concerned was undoubtedly referable to *Pseudogorgia godeffroyi* Kölliker (1870). The specimen, on which Kölliker described this species with a subtitle "eine Zwischenform zwischen den Gorgoniden, Alcyoniden und Pennatuliden" in 1870, was deposited at the Museum Godeffroy in Hamburg, and came from St. Vincent Gulf near the Investigator Strait. This octocoral, however, has never been recorded again for nearly a century and thus has long been forgotten and neglected wholly in recent systematic treatments of octocorals.

Concerning its systematic position, Kölliker himself considered it to be intermediate between Gorgonacea, Alcyonacea and Pennatulacea, but he did not suggest a family affiliation. Some of later authors have attributed it to the *Telesto*-allies, notwithstanding, for instance, the denial of the presence of direct connection between the lateral polyps and the axial canal of longitudinally extended gastric cavity of the axial polyp by Kölliker.

So, the rediscovery of this less-known Australian octocoral is indeed worthy of special mention, as it must have had offered difficulties in classification to earlier authors for its aberrant peculiarities that have resulted in its complete disappearance in the later literatures. And, it is in this same regard that the reinstatement of the present species, as circumstantial evidence, might contribute to the renewed investigation of the pathways of evolution in Octocorallia.

Materials and Habitat

All the specimens of the present octocoral have been collected exclusively in the waters of the eastern south coast of Australia. The bottom is sand or gravel.

Three groups of materials rendered for the present study are as follows.

Material 1.   Dorothea Island, Investigator Group, Great Australian Bight, 34 m in depth, sandy bottom where shell fragments, bryozoans and simple corals (*Platytrochus*) occur together. Collected by Mrs. Jeanette E. Watson, January 12, 1969. 7 specimens, mostly complete, were examined.

Material 2.   Off Kangaroo Island, Diving Survey Station 415 (35°25'S, 137°15'E),
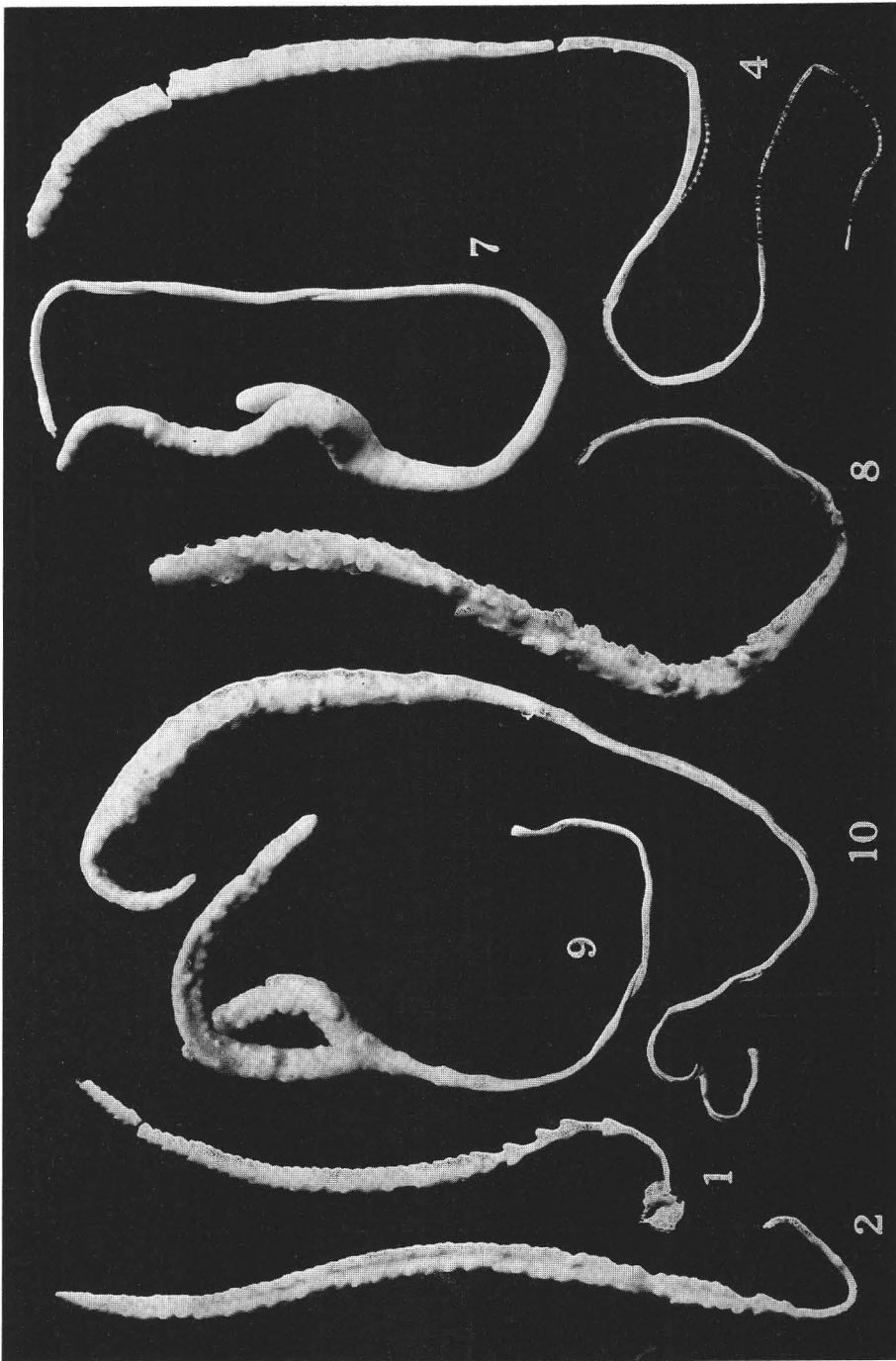
Fig. 1. Representative specimens of *Pseudogorgia godeffroyi*. Each figure shows the specimen number referred to in Table 1. ×1/2.
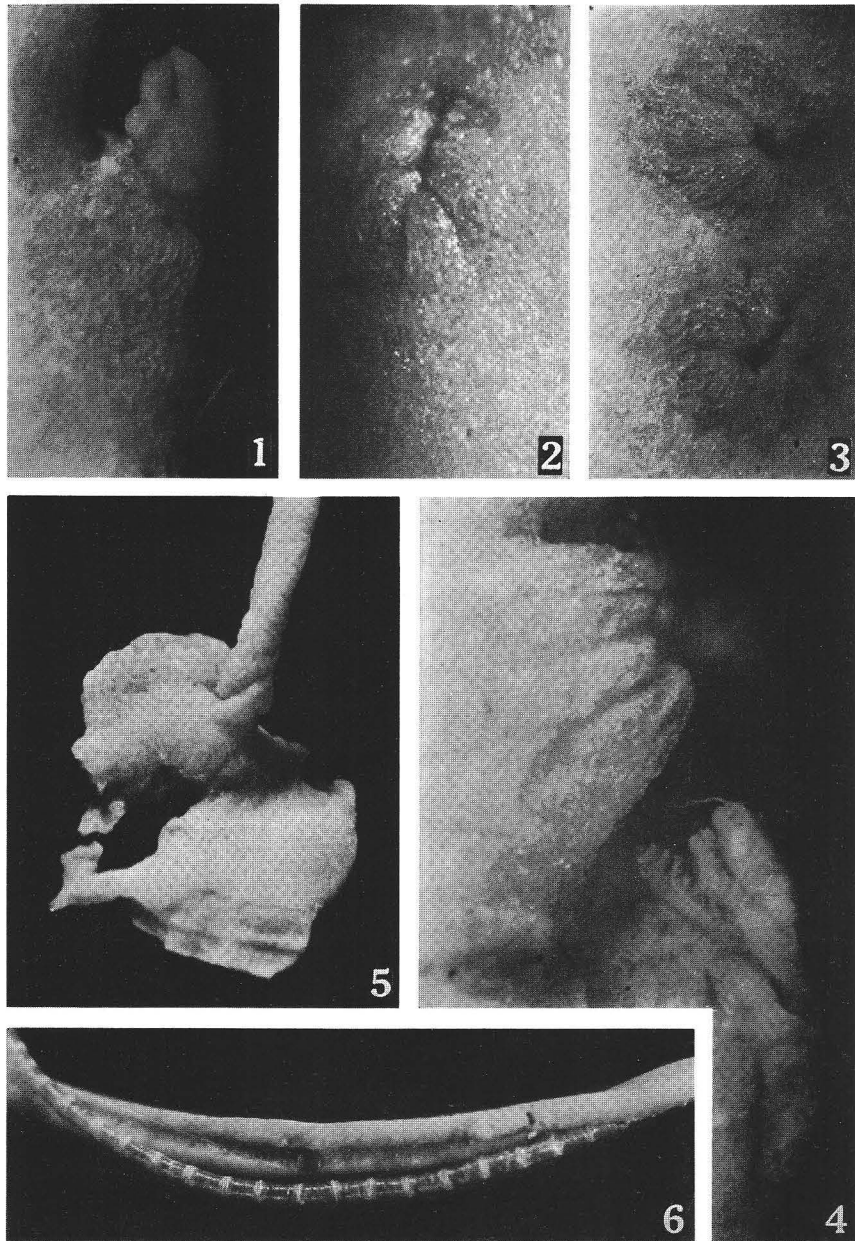
Fig. 2. Polyps and attachments. 1: lateral polyp, with tentacles slightly extended, of flattened colony (specimen no. 1); 2: lateral polyp, fully retracted, of flattened colony (specimen no. 3); 3: unprotruded lateral polyps, fully retracted, of cylindrical colony (specimen no. 4); 4: protruded lateral polyps, one of which with tentacles extended, of flattened colony (specimen no. 8); 5: basal attachment on to shell fragment˸ (specimen no. 1); 6: basal attachment along chaetopterid tube (specimen no. 4). 1–4: ×20; 5–6: ×4.

Investigator Strait, 30–45 m in depth, coarse sand bottom, heavily marked with ripples approximately 0.7 m apart by current (prob. 1 m/sec.), other fauna sparse, comprising bivalves, rarely brachiopods.   Collected by Mrs. Jeanette E. WATSON, January 24, 1971. 3 nearly complete specimens were examined.

Material 3.   Off Lakes Entrance, E. Gippsland Scallop Survey Station 200 (38°10'S, 148°E), Bass Strait, Victoria, 45 m in depth, gravel bottom with sponges (*Callyspongia elongata*), scallops (*Notovolva albida*), ascidians (*Pyura* sp.), current probably to 1.5 m/sec.   Collected by Gippsland Scallop Survey, date unknown, deposited in the National Museum of Victoria (7644/69), of which 3 incomplete specimens were examined.

Methods

For anatomical study of the internal structure of the colony, various parts were selected from the specimens which were fixed in formalin and preserved in alcohol of about 70%.   Materials were decalcified in TCA-formalin solution (9 parts of 5% trichloroacetic acid solution and 1 part of formalin) for 1 to 3 days according to the size of the material, then transferred to 90% alcohol, subsequently dehydrated in terpineol and embedded in paraffin (m. 55–59°C).   Undecalcified materials were also dehydrated and embedded.   Sections were cut at 10–15 μ and stained with Heidenhain-azan (azocarmine for 10 minutes, phosphotungstic acid for 15 minutes, and aniline blue orange G for 10 minutes) or Ehrlich's hematoxylin and eosin.

Description of New Materials

KÖLLIKER (1870) has already given a remarkably detailed description of the anatomy of this octocoral, and the present observation confirms his result for the most part.   There are, however, some erroneous and misleading statements in his de-scription, as well as some characteristics not mentioned, partly because of his de-scription being based on a single specimen.   For instance, the asulcal (dorsal) mesenterial filaments of the axial polyp were called erroneously as *'ventral'* septa by KÖLLIKER, since he named the concave side of the capitulum as *'dorsal'* side, neglecting the structure of the axial polyp.   This is also known from his figure (Fig. 12), in which he illustrated gonads on the very side of the axial canal, that he named *'dorsal'*.

Since the work of KÖLLIKER (1870) is not known well, the descriptions of the external form and anatomical structure of the colony are reproduced here, based on the newly obtained materials to restore and complement KÖLLIKER's original description.

(1)   External Morphology

General appearance: The colonies are typically unbranched and consist of the blade-

like upper part, i.e. the capitulum, and the filiform flexible lower part, i.e. the sterile stalk.   The relative length of the capitulum to the stalk varies among specimens, nearly 1:1 to 20:1, largely depending on disk-shaped or sheath-shaped basal attachment. There are only a few fully expanded lateral polyps in the specimens.

Capitulum: The capitulum is flattened dorsiventrally, narrow, lanceolate in form and bendible (not rigid at all).   It attains to a size of about 40 cm in length, 7–12 mm in width and 3–5 mm in thickness in the larger specimens.   The central area is slightly sunken on one flattened surface and is relatively raised on the other.   In the narrower and thinner terminal part, the flattened surfaces are slightly raised axially as a straight fold, corresponding in its position to the extended gastric cavity of the axial polyp. The edge is rimmed by the polypal verrucae on both sides, whereas the flattened surface is mostly naked.   These polypal verrucae are longitudinally arranged more or less alternately to the plane of flattening and are inclined upwards somewhat obliquely.

In some specimens, however, there are several polypal verrucae scattered on the flattened surfaces of the capitulum.   Further in some specimens, which have somewhat cylindrical capitulum, polypal verrucae are distributed over the whole surface of the capitulum around.   In this case, the polypal verrucae are less prominent.   The diameter of the capitulum is rather uniform, varying from 7 mm to 12 mm across.

In a few specimens, either blade-like or rod-like, the capitulum is abnormally forked, not in a manner of branching as seen usually in most of the Telestaceans. Both branches may attain to a fairly remarkable length.

Polyps: The polypal verrucae, namely anthosteles or calyces, are conical in form and measure about 3 mm in length by 2 mm in diameter at base in the well-protruded ones. Their wall is granular, being thickly covered with cortical spicules, and is 8–lobed distally.   In full-expanded anthocodiae of the lateral polyps, the tentacles are seen bearing about 10 pairs of simple pinnules, but none of spicules at all.

In complete specimens, the uppermost end of the capitulum, slightly truncated, measuring about 1.5 mm wide, is obviously opened by the mouth of a single terminal polyp extending downward axially and surrounded by 8 lobes, as in the acorn-shaped lateral polyps, although the tentacles are deeply retracted in hitherto examined specimens (vide infra on the internal structure).

Stalk: The stalk lacks polyps.   It is exclusively long, filiform, flexible and nearly cylindrical in section, about 2 mm across, tapering slightly downward.   The basal part of the stalk is different in appearance among specimens, depending upon the object on which they settle.   When settled on bivalved shell fragments, it forms a thin membranous disk, about 1 cm across.   When settled on chaetopterid tubes, probably of *Phyllochaetopterus socialis* CLAPARÈDE, however, it forms an elongate sheath hollowed on sulcal side of the axial polyp to embrace the tube.   The basal frill of the sheath, when freed from the chaetopterid tube, appears more or less rugose inside, apparently like the hollowed basal attachment of such scleraxonian gorgonaceans as *Solenocaulon, Solenopodium* and *Tripalea*.

Table 1. Measurements of specimens.

Specimen		Shape	Attachment	Branch	Capitulum Length (mm)	Maximum width (mm)	Maximum thickness (mm)	Stalk Length (mm)	Average diameter (mm)
Material 1	1	flattened	shell fragment	no	109	6.7	2.7	56	1.4–1.8
	2	"	hard object (?)	"	170	8.3	2.6	64+	2.1–2.5
	3	"	" "	"	100+	5.7	2.3	48+	1.5–2.1
	4	"	chaetopterid tube	"	133	8.4	4.1	285	1.2–2.7
	5	"	" "	"	178+	9.8	6.0	188	1.8–2.8
	6	"	" "	longer	69+	7.5	2.8	105	1.3–2.0
				shorter	6	5.8	2.1		
	7	cylindrical	" "	longer	137	12.7	9.3	195	2.8–3.2
				shorter	27	6.3	3.8		
Material 2	8	flattened	" "	no	175+	11.3	3.3	99	2.2–3.0
	9	"	" "	longer	120	8.6	4.7	142	2.0–2.6
				shorter	48	8.9	4.6		
	10	cylindrical	" "	no	142	12.0	11.0	227	2.2–2.5
Material 3	11	flattened	unknown	"	406+	7.8	3.6		
	12	"	"	"	305+	10.4	4.5		
	13	"	"	longer	410+	12.8	5.0		
				shorter	30	5.8	2.5		

Colour in alcohol: The capitulum and stalk in all specimens preserved in alcohol are uniformly ivory buff, but the extended anthocodiae are translucent and colourless.

Measurements: Measurements of the specimens examined are shown in Table 1.

(2) Internal Structure

Axial polyp: The most outstanding feature of the colony is the presence of a single axial polyp, which opens its mouth at the tip of the capitulum and extends its gastric cavity as an axial canal down the whole colony throughout. The axial polyp is functional, having well-developed tentacles and gonads. Its main body is slightly elongated as compared to the lateral polyps, measuring about 2 mm across. The stomodaeum reaches to a depth of about 4 mm from the mouth in retracted condition. The siphonoglyphe is not clearly seen. The mesenteries bear on their sulcal (ventral) faces the large muscles.

In the longitudinally extended axial canal are seen the mesenterial filaments, of which the sulcal (ventral) and particularly the asulcal (dorsal) ones are long. They continue down to the point where the axial canal breaks into three smaller canals. This branching of the axial canal appears as partitioning by the asulcal mesenterial filaments fusing with the canal wall of opposite side. This point corresponds to the lower end of the capitulum. Only the lateral two of them are conspicuous and always lead straightly down to the base of the stalk, keeping nearly the same size. The narrow asulcal one is also usually continues down to the base of the stalk, but seldom disappears into solenia some way down and a canal of similar size originating from a gastrodermal solenium takes the place of it.

In the specimens of which the capitulum is abnormally branching, both branches have an axial polyp. The canals of these axial polyps are never united directly together, and one of them disappears into solenia somewhere below the branching region. In the case the branch is short and knob-like in form, one of the lateral polyps at the base of the branch is seen divided into two polyps.

Lateral polyps: The lateral polyps, arranged biserially or circumscribingly along the axial polyp, are exclusively short and acorn-shaped, 7.5 mm in length by 2.5 mm in diameter. They are buried almost completely in the coenenchyme and are nearly reaching the axial canal at their bottom, being declined upwards. The asulcal side of these lateral polyps always faces to the axial canal inward. They are connected each other through solenia and also with the axial polyp, particularly evidently in the upper part and in the branching region of the capitulum. A few polyps in the uppermost part of the capitulum are small, seemingly not well-developed, and a few lowest seemingly degenerating.

Medulla and cortex: The horny or calcareous rigid axis (in the sense of BAYER, 1961, or others; 'medulla' in the sense of VERSEVELDT, 1940) is wanting.

Three layers of the coenenchyme are distinguishable, although the boundaries of them are rather indistinct and obscure. The outer cortical layer, a very thin surface
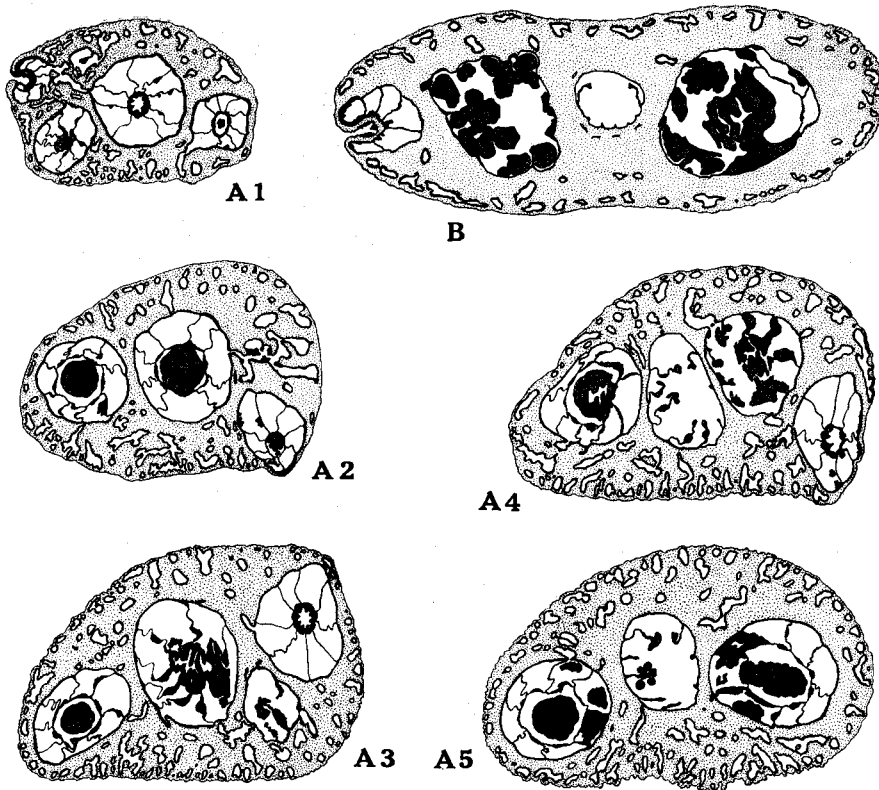
Fig. 3a. Arrangement of polyps and gastrodermal solenia in cross section of the colony. A, B, C,...
F correspond to the parts designated as *a, b, c,* ... *f* on the left figure of Fig. 5 respectively.
Note that, in one specimen (E2, E1 and D), the canal which appears to be the asulcal stalk canal
(on E2) is traced upward (through E1) and found to be originated from a solenium (asc on D).
×13.

layer of the cortex, is marked off by the gastrodermal solenia lying subjacent to the
surface, and is devoid of large gastrodermal solenia. The inner cortical layer, a
thick layer occupying the most part of the coenenchyme particularly in the capitulum,
is perforated by gastrodermal solenia, especially abundantly in the peripheral part.
All the lateral polyps are embedded in the cortex and never extend into the medulla,
except the gastrodermal solenia connecting them with the axial canal, naturally as the
cortex is defined as 'the layer of coenenchyma in which the coelenterons are embedded'
(VERSEVELDT, 1940). However, the medulla in this species is indeed penetrated by
the long extended coelenteron of axial polyp!

　The medulla, which takes the form of a thin layer surrounding the axial canal in
the capitulum and of a massive central core occupying almost half the size in the stalk,
is rarely penetrated by gastrodermal solenia, except those originating from the axial
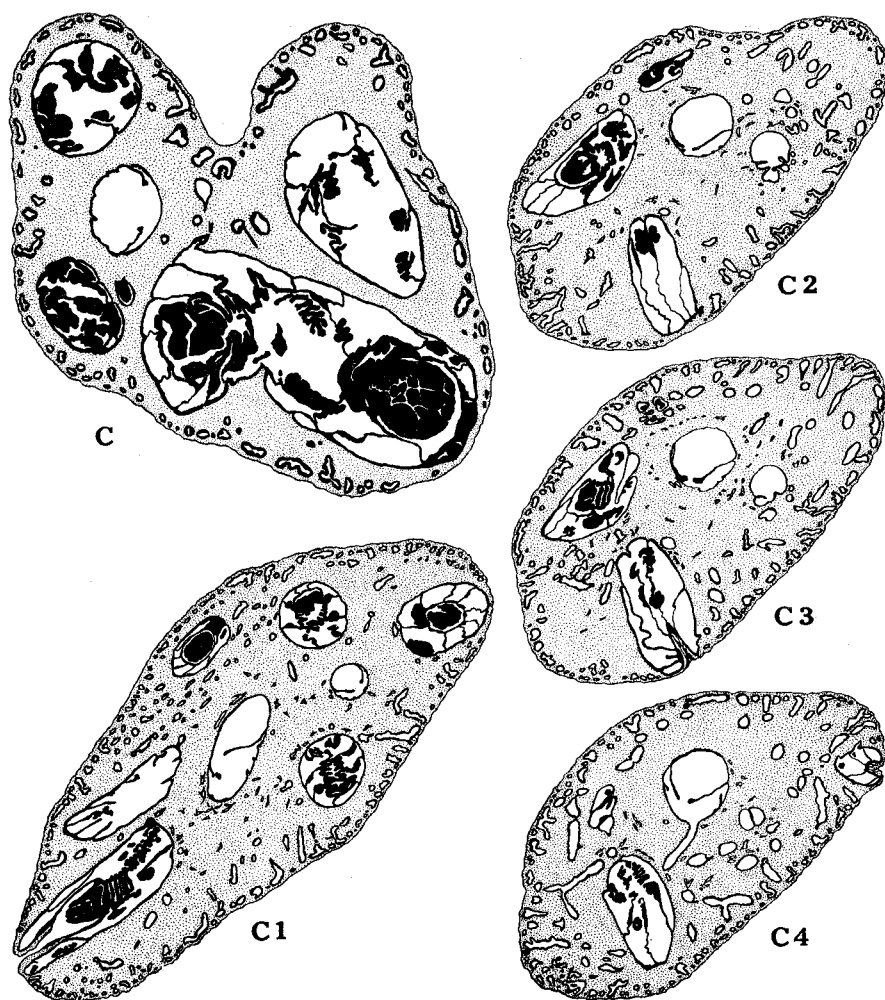
Fig. 3b. Arrangement of polyps and gastrodermal solenia in cross section of the colony.

canal transversely. The horny cells, which resemble in appearance to those illustrated, for example, by KÜKENTHAL (1919) for *Melitodes flabellifera* (Tafel L) or by VERSEVELDT (1940) for *Paragorgia arborea* (Figs. 5 or 8), are embedded character-istically in this layer and are extremely abundant in the stalk. The horny substance secreted around the cells is stained strongly red by azan, as well as the cells themselves more weakly.

The boundary solenia (in the sense of VERSEVELDT, 1940, separating the cortex from the medulla) are not distinguishable.

Canal systems: The gastrodermal solenia are distributed particularly densely in the outer part of the inner cortical layer of the capitulum. They ramify and fuse together
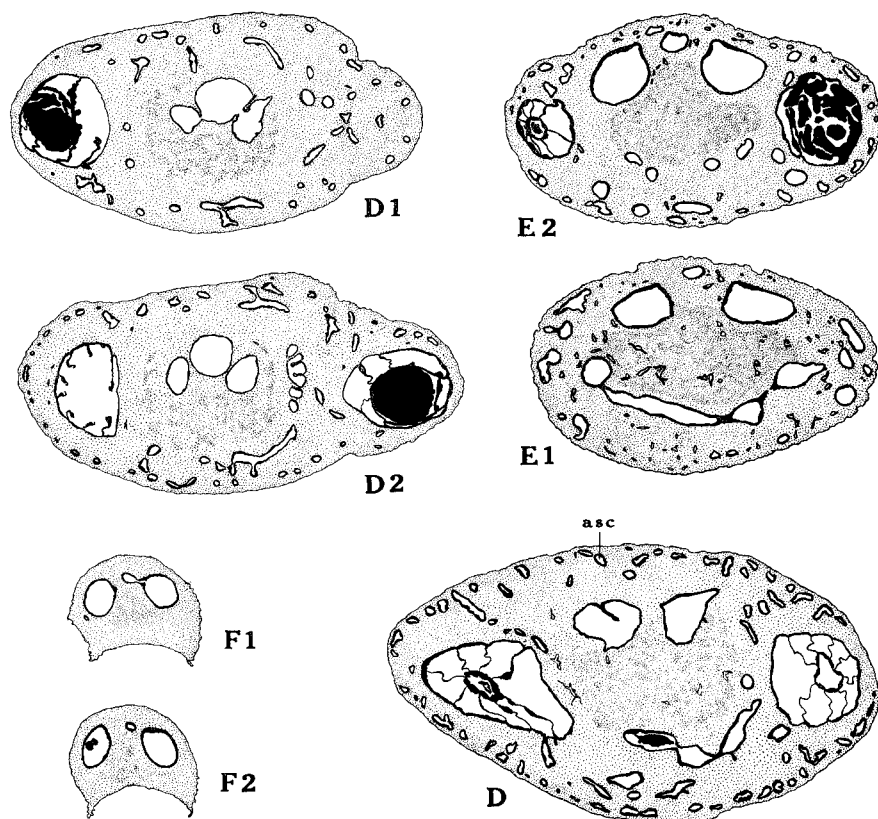
Fig. 3c.　Arrangement of polyps and gastrodermal solenia in cross section of the colony.

again and again to form a complicated network and run chiefly longitudinally under the outer cortical layer in the capitulum.　There are, however, no solenia running down straight throughout the length of the capitulum.

In the inner part of the cortex, the gastrodermal solenia are fewer and run rather transversely, ramifying and fusing as well.　There are no solenia running longitudinally between the cortex and the medulla, which are distinguishable as the so-called boundary solenia.　The medulla is perforated by much fewer solenia.

In the stalk, the gastrodermal solenia are quite few and chiefly run in a longitudinal direction.

The gastrodermal solenia pass into the axial canal fairly frequently, particularly in the terminal and the branching region, and some of them are directly connecting it with lateral polyps.　These lateral polyps are also connected by the complicated network directly or indirectly at various parts of their body with each other.

The gastrodermal solenia are distinguishable as wide and narrow canals.　The
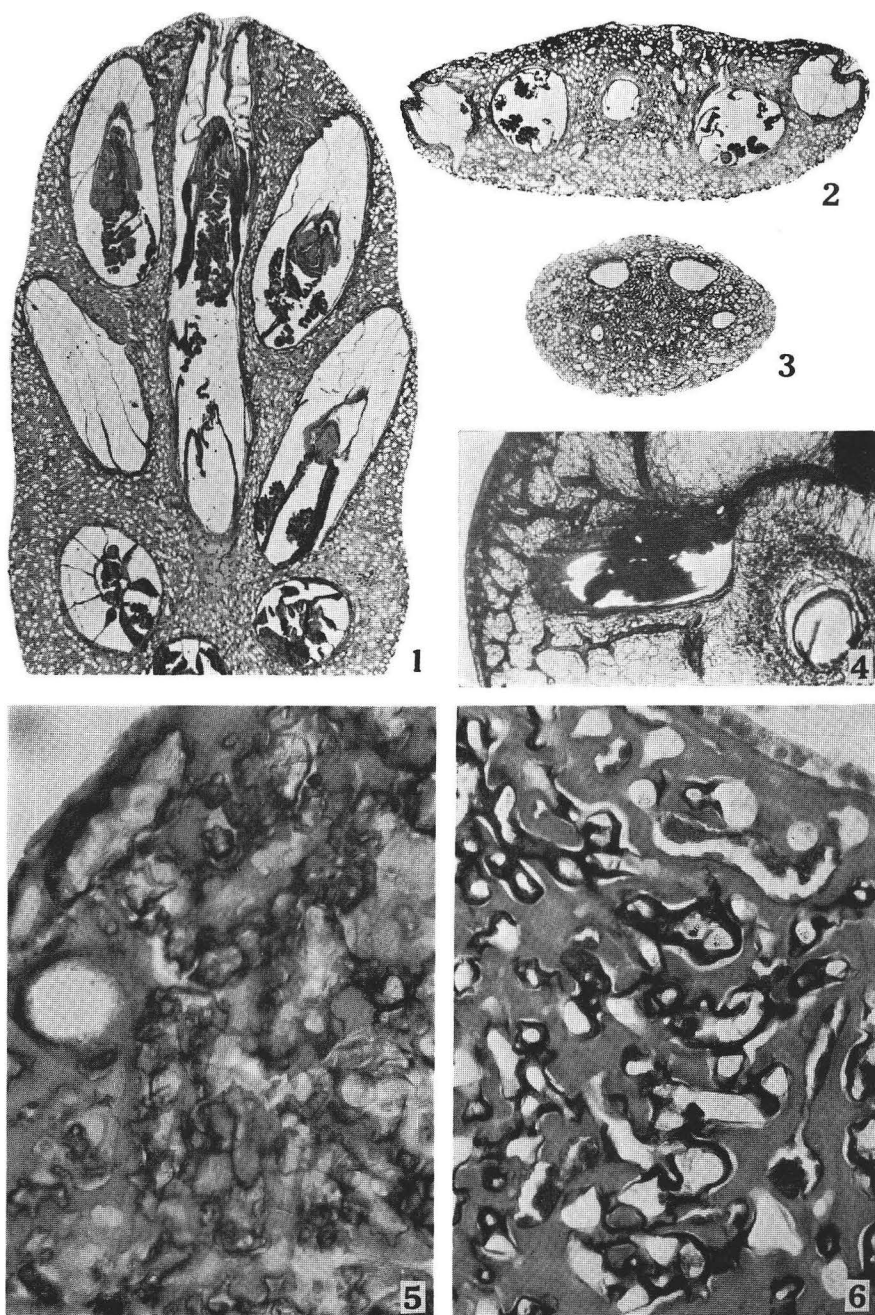
Fig. 4. Sections of colonies. 1: sagittal section of terminal part of capitulum, decalcified, to show the axial polyp, 12μ thick, azan preparation; 2: cross section of capitulum, decalcified, 12μ thick, azan preparation; 3: cross section of stalk, decalcified, 12μ thick, azan preparation; 4: cross hand section of cylindrical capitulum, decalcified, to show solenia and cell strings, safranin-light green preparation; 5: a part of capitulum, undecalcified, to show spicules in mesogloea, 15μ thick, haematoxylin-eosin preparation; 6: cells with horny substance around in stalk, 12μ thick, azan preparation. 1–3: ×10; 4: ×5; 5–6: ×150.
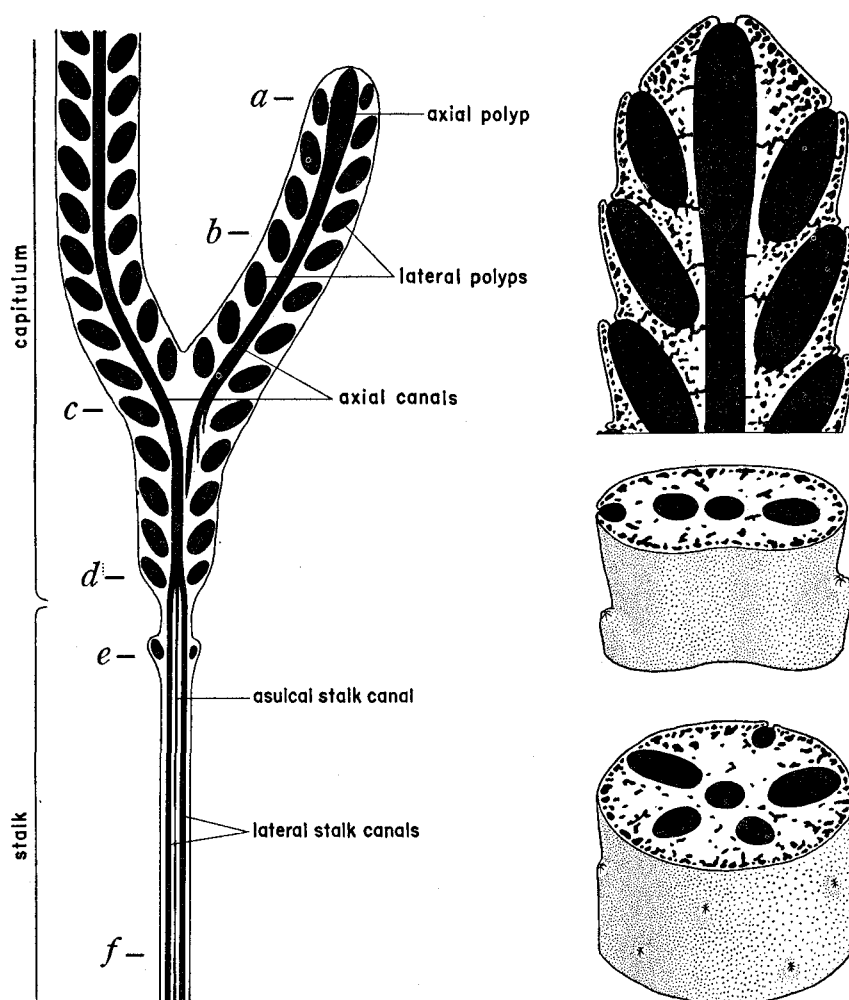
Fig. 5.   Schematic representations of the structure of the colony of *Pseudogorgia godeffroyi*.   Left:
arrangement of polyps and axial canals.   Right: arrangement of polyps and gastrodermal solenia
of terminal part in sagittal section (upper), of proper flattened capitulum in cross section and
lateral view (middle), and of proper cylindrical capitulum in cross section and lateral view (lower).

wide solenia are about 0.1 mm in diameter and the narrow solenia are about 0.03 mm
in diameter.

Spiculation: The spicules are different in shape, according to the region of the colony.
Generally speaking, in the cortex of the capitulum, spicules are mostly of tuberculate
spindles bluntly ended; the spicules with which the thin outer layer is densely packed
are belted more or less clearly and larger (nearly reaching to 0.25 mm in length), while
those of the inner layer between the lateral polyps are rather loosely packed and are
smaller (up to 0.2 mm in length).   In the medullary layer around the axial canal of
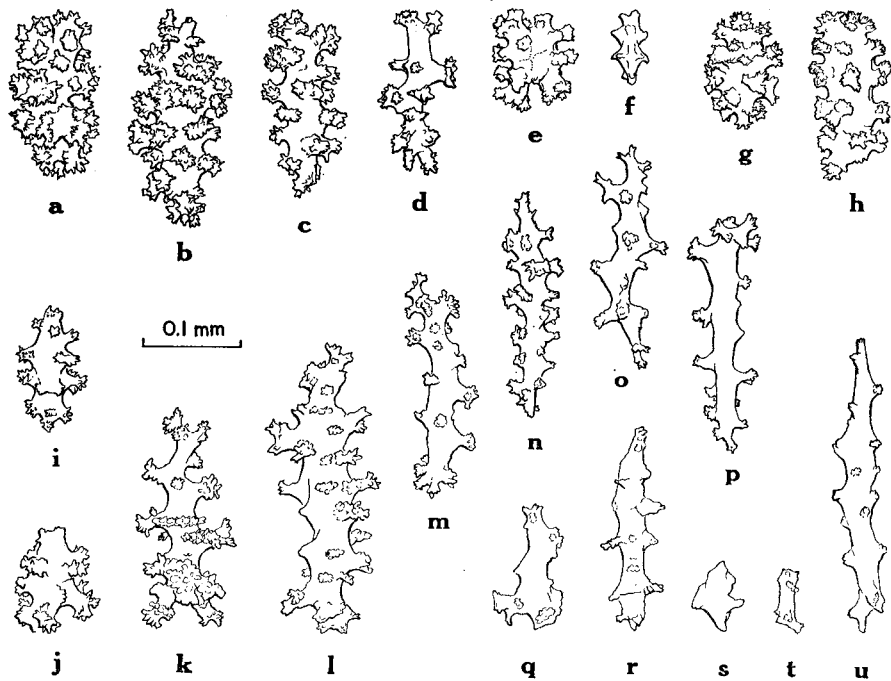
Fig. 6. Spicules from various parts of the colony. a-f: outer cortical layer of capitulum; g-j: inner cortical layer of capitulum; k-p: medullary layer of capitulum; q-u: stalk. ×130.

the capitulum and in the coenenchyme of the stalk are contained predominantly longer spindles (exceeding 0.3 mm in length), having more compound tubercles in the capitulum than in the stalk.

Such radiate or branching rods, as seen in most scleraxonian gorgonids and telestaceans are not found in the deeper layer around the axial canal.

Historical Review of the Systematic
Treatments of *Pseudogorgia*

As far as we know, the genus *Pseudogorgia* appears only in a few literatures. These literatures are exclusively those earlier than 1930, and in recent classifications *Pseudogorgia* is not only not referred to, but also does not seem to be taken into consideration.

KÖLLIKER (1870), in his original description of the species *Pseudogorgia godeffroyi*, discussed its similarities and dissimilarities to Alcyonacea, Gorgonacea and Pennatulacea. For example, he expresses himself: "Steht somit auch *Pseudogorgia* mehr zwischen Alcyoniden und Pennatuliden in der Mitte, so erinnert sie doch auch

an die Gorgoniden, vor Allem durch den Habitus, die seitlichen Polypen und den Bau des Sarcosoma und würde, wenn der axiale Polyp nicht wäre, als eine typische Briareacee bezeichnet werden dürfen" (p. 28).   He must have met with the difficulties in assigning it to the right place in Alcyonarian classification and suggested only that it represented an ancestral form of the Pennatulid group, especially closely related to *Virgularia* amongst the members, and was an intermediate between Alcyonacea, Gorgonacea and Pennatulacea.

STUDER (1887, p. 13) and WRIGHT and STUDER (1889, pp. 253–254) attributed it to the family Cornularidae DANA (now Clavulariidae) of Alcyonaria, together with varied genera, such as *Cornularia, Telesto, Coelogorgia, Anthelia, Callipodium*, etc. In STUDER's paper, however, this is not clearly stated in his list of genera belonging to Cornularidae (p. 11), but is only suspected from his schema showing the relationship between the genera he grouped into the family Cornularidae DANA (p. 13).   In this he places *Pseudogorgia* as related on one side to *Gymnosarca* KENT (an enigmatic Briareid gorgonacean, probably related to *Anthothela*) together with *Telesto* of the Telestacea, to which it is also indicated to be related, and to the Pennatulacea on the other.   This is expressed in his statements on the position of the Holaxonia as follows: "Sie(=die Holaxonier) dürften sich am besten auf Cornulariden von der Form der *Telesto* zurückführen lassen, diese leiten einentheils durch *Pseudogorgia* zu den *Pennatulacea* über, anderentheils direkt, oder durch *Coelogorgia* zu den Holaxoniern" (p. 37).   Concerning *Pseudogorgia* itself, however, he gives nowhere any account.

KÜKENTHAL (1906, p. 99) appears to follow STUDER's view on the position of *Pseudogorgia*.   Although he makes no mention on this species at all in the text, he places it, as well as *Coelogorgia*, near *Telesto* in the schema illustrating the genus relationship, as detaching at the root of the branch leading from *Scleranthelia* (now referred to the Clavulariidae of the Stolonifera) to the Holaxonia and Pennatulacea through *Telesto*.

HICKSON (1930) came last to deal with *Pseudogorgia* and implied the change of its position.   Since the establishment of a special family Telestidae by MILNE-EDWARDS et HAIME (1857), MAY (1900, pp. 53–54) and most of the later authors followed them. For this family, HICKSON (1930) erected an order Telestacea, separating from the Stolonifera (including the families Cornulariidae and Clavulariidae), Alcyonacea and Gorgonacea, to which he referred *Pseudogorgia*, together with the genera *Telesto, Coelogorgia* and *Pseudocladochonus*, rather customarily or conveniently.   Prior to the establishment of a new classification of the Alcyonaria, HICKSON (1916) dissented emphatically BOURNE's (1900) attempt to unite the Telestidae with the Pennatulacea in an order Stelechotokea.   He claimed that the Pennatulacea should be kept intact and wrote: "I regard the Telestidae has a highly specialised family of Alcyonacea which may have arisen independently from the Stolonifera but do not in any way represent an ancestral stage of the Pennatulacea" (1916, p. 25).   Eventually, he opposed KÖLLIKER's (1870) opinion as mentioned above, but, again, the reasons for this re-

markable change of the position of the genus *Pseudogorgia* were not given.

In connection with this, it may also be mentioned that HICKSON agreed with KÜKENTHAL in putting aside KÖLLIKER's opinion as to a linkage through *Pseudogorgia* and in placing the origin of the Pennatulacea among the more primitive forms of the Alcyonacea such as radially symmetrical *Anthomastus*, as equivalent to *Lituaria* belonging to the Pennatulacea, instead of bilaterally symmetrical *Virgularia* (cf. KÜKENTHAL, 1910, pp. 563–570).

Systematic Position of the Genus *Pseudogorgia*
and the New Order Gastraxonacea

The systematic position of *Pseudogorgia godeffroyi* is really a matter of discussion. Certainly it has in some respects similarities to the order Pennatulacea: two parts of an upper polypiferous capitulum and a lower sterile stalk clearly distinguishable in the colony; the presence of an axial polyp whose gastric cavity is elongated to reach the base of the stalk; the division of the gastric cavity of the axial polyp; etc. On the other hand, it has also many characteristics distinct from the Pennatulacea: the lateral polyps, almost completely embedded in spiculiferous, not fleshy, coenenchyme, of a single kind (monomorphic), instead of invariably at least two kinds; the lateral polyps not formed by direct budding from the axial polyp; the axial polyp opening at the distal tip of the colony, instead of "dass der als axialer Polyp aufgefasste Stamm selten an seinem Ende in einen Polypen mit Mund und Magenrohr ausläuft sondern ein rein vegetatives Individuum darstellt, das am Ende blind geschlossen ist, resp. immer auf dem Stadium eines Stolonen bleibt" (STUDER, 1887, p. 37) in the Holaxonia and Pennatulacea; spicules in form not of smooth or three-flanged rods or needles; the basal part of attachment by no means free, not anchored in a soft substratum and uncapable of some movement; the total absence of any solid axis; etc.

As formerly suggested by the senior author (UTINOMI, 1957, 1958a), the soft bottom inhabiting *Bellonella* is a cylindrical Alcyonacean and represents a primitive form of the Alcyonacea with fleshy texture and many polyps lengthened down to the base. For example, *B. rigida* PÜTTER has sometimes been treated as a member of the Pennatulacea on account of its apparently similar shape and occurrence on the soft sea floor. Similar case may often been met with for some genera of the Gorgonacea, occurring on the soft sea floor, such as *Filigella* (=*Elasmogorgia*) and *Menella* of the Paramuriceidae (UTINOMI, 1958b, 1961). Apart from the internal structure, especially with regard to the canal system, the simplicity and flexibility of the stem as in some cases of other Gorgonaceans probably represent a case of convergence, due to the occurrence on the soft bottom, rather than of genetic relationship. This assumption is more strengthened by a comparison with most of the pennatulids and some of the alcyoniids dwelling on similar habitat.

The order Telestacea, represented by *Telesto* LAMOUROUX, *Telestula* MADSEN,

Coelogorgia MILNE-EDWARDS et HAIME, *Paratelesto* UTINOMI and *Pseudocladochonus* VERSLUYS, is an isolated group, as considered by HICKSON (1930) and later by MADSEN (1944) and BAYER (1961).   In recent concept of the Telestacea, they are usually stoloni-ferous, arborescent octocorals and the tall primary polyps arising from the stolon produce the similarly constructed, elongate, cylindrical daughter polyps, which often become the branches of the first order and further produce similarly constructed secondary polyps and then those of higher orders, when much developed.   Even so, however, they do not grow beyond 20 cm in height (e.g. *Coelogorgia palmosa*).   The outer surface of the body walls, either the axial or the lateral polyps, is always provided with eight spiculiferous longitudinal ridges all throughout; internally, the axial gastric cavity is surrounded by eight thin mesenteries and either open to the base or filled with mesogloeal spicules in the lower part (in *Telestula*).   They usually occur on hard bottom such as rocky reef or stones (UTINOMI, 1973, pp. 145–155).

Apart from the external appearance and development of the colony, *Pseudogorgia* shows certain features of resemblance to the Telestacea in the existence of more or less well-defined axial polyps, the modes of arrangement of polyps, the entire absence of a solid axis, etc.   Yet, the differences between them are so remarkable as to refuse *Pseudogorgia* from inclusion in the Telestacea.   In *Pseudogorgia*, the axial canals (gastric cavities of axial polyps) of branches of a colony never unite directly, the lateral polyps are uniformly short and formed of dome-shaped calyces and anthocodiae retractile into the coenenchyme of the stem like the gorgonaceans, and they are con-nected with the axial coelenteric canal only by gastrodermal solenia.   Unlike the telestaceans, also, the outer surface of the body wall of the polyps, either axial or lateral, is plainly granular and no creeping stolon is formed at the basal attachment.

The order Stolonifera is the colonial Alcyonaria with a membranous or ribbon-like basal stolon, from which only the cylindrical or blunt-conical polyps spring, thus resulting the complete absence of secondary polyps budding off from the body wall of other polyps.   It is self-evident that, by this definition of the Stolonifera, *Pseudo-gorgia* is by no means referable to it.

In the order Alcyonacea, the colonies are usually fleshy, thick and internally com-posed of a number of gastric cavities of the primary polyps forming together a bundle. One character which the Alcyonacea have in common is, according to HICKSON (1930), "that the body-cavities of the primary polyps of each colony extend from the surface to the base, and the body-cavities of the secondary polyps are long" (p. 242).

Despite the certain similarities, such as the existence of an axial polyp extending from the base of the colony to the surface of its tip, the supposed formation of lateral polyps from solenial system, and the absence of clearly defined rigid axis, the differences between the Alcyonacea and *Pseudogorgia* are far pronounced.   In *Pseudogorgia*, there is only one axial polyp in a colony, the gastric cavity of which is extending to the base of the colony, the lateral polyps are uniformly short and the coenenchyme is not fleshy at all.

The extension of polyps in the terminal part of the colony is found in some different groups of the Gorgonacea, too. HICKSON (1930) pointed out this as follows: "Although the character of long body-cavities is common to all Alcyonacea, it cannot be used to distinguish absolutely the Alcyonacea from the Scleraxonia, because some of the latter have, or appear to have, also long body-cavities" (p. 242). *Briareum* and *Paragorgia* are the examples as such, for which VERSEVELDT (1940) states: "The terminal zooids of *Briareum* and *Paragorgia* proceed in so-called coelenteric canals, which have to be considered as parts of the coelenterons, and not as solenia" (p. 126). In *P. arborea*, "the three middle-most terminal autozooids penetrate the stem for a different distance" and "the left one passes into a wide medulla-canal, which is traceable far basally" (VERSEVELDT, 1940, pp. 26–27). In *Tripalea*, too, the similar features are recognized as bearing some importance for the determination of its systematic position. BAYER (1961) considers: "The extension of the polyps as long coelenteric canals is strongly suggestive of *Briareum*, but in *Tripalea* the medulla takes form between the uppermost polyps and the canals lie in a ring around it, becoming farther and farther apart as the medulla increases in diameter proximad. The circular canal system is not continuous since it consists of coelenteric extensions of polyps that arose at different levels in the colony; it is, however, a boundary system in the broad sense and *Tripalea* must, for the time, be reckoned among the Anthothelidae. Its long coelenteric canals, arranged in a ring between cortex and medulla, give it a position intermediate between *Briareum* and the anthothelid genera" (p. 70).

The order Gorgonacea is characterized by the presence of clearly defined axis. This order has been divided by STUDER (1887) into two suborders (originally sections), Scleraxonia and Holaxonia, by the nature of the axis. In the Holaxonia, the axis is made up of amorphous horny material, not of calcareous spicules, and is occasionally penetrated by a chambered central chord. The axis is proved by KINOSHITA (1913) in the Keroeidae, for instance, to be produced by the axial epithelium which is continuous in origin with the basement ectoderm, and, as a slightly different opinion on the origin of the axis, HICKSON (1930) admits that there does not seem to be any reason to doubt the truth of the older view that the axis is entirely a product of the ectoderm. Whatever the difference in opinion may be, no statements or assumptions have ever been made that the chambered central chord is continuous with or is developed from the gastric cavity of any polyp in the colony.

Among the monomorphic Scleraxonia, the family Anthothelidae is known to represent the connecting-link with the Stolonifera on one hand and the Alcyonacea on the other. The principal genera belonging to this family are *Anthothela*, *Iciligorgia*, *Solenocaulon*, *Alertigorgia*, *Tripalea*, etc. The original definition given for this family by BROCH (1916) concerning the axial part of the colony runs as follows: "Die achsialen Gewebe sind von einem Kreise longitudinal verlaufender Kanäl umgeben, die nicht als Fortsetzungen von Gastralhöhlen von Polypen aufgefasst werden müssen" (p. 14). The medulla is rarely perforated by the gastrodermal solenia, in contrast to the

Briareidae, in which "die achsialen Partien der Kolonie, die gegen die Rinde nicht deutlich begrenzt sind, werden von primären Längskanälen durchzogen, die als Fortsetzungen von Gastralhöhlen von Polypen aufgefasst müssen" (BROCH, 1916, p. 14). The Paragorgiidae is much alike the Briareidae, except that their polyps are dimorphic, and the central axis is perforated by gastric canals of terminal zooids (AURIVILLIUS, 1931, p. 10).

Pseudogorgia godeffroyi, indeed, reminds us the Gorgonacean forms such as *Tripalea, Alertigorgia* or *Solenocaulon* in its general external appearance. The habit of the present species of growing on the chaetopterid tubes resembles that of *Tripalea clavaria* (=*Suberia clavaria* STUDER, 1878) of growing on other Gorgonaceans. The hollowed sheath of the stalk thus formed on attachment in the present species shows some similarities to the structure of hollows in *Solenocaulon*. Yet, again, the existence of the axial polyp and its extended gastric cavity as an axial canal, the absence of the well-defined axis and the absence of the boundary canals surrounding the medulla, all distinguish decidedly *Pseudogorgia* from the Gorgonacea.

Pseudogorgia godeffroyi is thus so apparently marked off from other Octocorallians by structure of colonies, particularly the arrangement of polyps and canal systems. It seems to us that the differences in these characters far outweigh in importance the features of resemblance, if we consider that the arrangement of polyps or "the form of growth of the colony as a whole" is "one set of characters which sedentary and colonial organisms, such as the Alcyonaria, possess and the bilaterally symmetrical animals do not" (HICKSON, 1930, p. 230), and that the Octocorallian orders are, as is seen in BAYER's (1956, 1961) classification, for example, distinguished significantly by the mode of development and arrangement of polyps.

It is, of course, neither impossible nor perhaps improbable to derive the particular type of arrangement of polyps in *Pseudogorgia godeffroyi* from some of those in other Octocorallians. Needless to say, the transformation thus thought of is meaningless unless it is in some respects implied by the actual way of formation of the colony. We have at present not enough knowledge on the development of the colony, and it is strongly needed for the determination of the relationship of the present species to other Octocorallians. However, as far as we can deduce from the anatomical features of the colony we have examined, the lateral polyps do not bud off directly from the extending axial polyp, which penetrates the medulla at its middle, although they are connected with it by direct or complicatedly anastomosing solenia. As a matter of fact, it seems to us that none of the Octocorallian orders are relevant to include *Pseudogorgia godeffroyi* as their specialized forms.

If the classification of the Octocorallia is still an artificial one and the consideration on the convenience of the systematist influence our choice, as HICKSON (1930) expressed, the proposal of placing the present species, *Pseudogorgia godeffroyi*, in a new separate order from other Octocorallian orders generally accepted at present, instead of restoring it to its place in the Telestidae in wider sense or the Telestacea, deserves the advantage,

at least, for practical purpose to avoid the misleading ammendments of their defi-
nitions. As a conclusion, until much knowledge on the present species, as well as on
other Octocorallians, will be accumulated, we dare to propose to establish a new
family Pseudogorgiidae and further a new order Gastraxonacea for this species,
whose known distribution seems to be at present confined to a small area in coastal
waters of the eastern South Australia, admitting that order and family names are
perhaps only superfluous when, as in the present case, they are represented by a single
species.

Order **Gastraxonacea,** ord. nov.

Polyps clearly distinguishable into a single axial polyp with extended gastric cavity
and a number of lateral polyps with short gastric cavity, at least in a branch when
colony branched; elongate gastric cavity of an axial polyp penetrating to the base
of the colony at its middle; without horny or calcareous axis or central medulla
composed of spicules, either free or inseparably fused; without creeping stolon.

Family **Pseudogorgiidae,** fam. nov.

Same as the order Gastraxonacea.

Conclusion

Summarizing the above, this new family or order, though of a small octocorallian
group, is appropriately regarded to be intermediate in structure between Telestacea
and Gorgonacea. It may provide a connecting link between the orders Alcyonacea
and Scleraxonian Gorgonacea. The order Telestacea, on the other hand, may
represent a direct offshoot of the primitive order Stolonifera, rather than of the other
evolved orders mentioned above.

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DISCUSSION

Werner: Has anybody seen the species alive?

Harada: Mrs. Watson has collected some alive specimens from the bottom by diving.

Thiel: Do you think that the axial polyp could function as a hydrostatical organ?

Harada: The extended axial canal of the axial polyp seems to be functional for water circulation, since it has mesenterial filaments for the most part of its length, but it is not certain without examining the living animal whether it gives the hydrostatic support to the colony.   As far as is seen from the preserved specimens, the colony retains enough support with its spicules and coenenchyme.